Primitive fossil flatworm from Alaska: New evidence bearing on ancestry of the Metazoa

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ABSTRACT

A well-preserved microscopic fossil flatworm, Brabinthes churkinii (new genus, new species), has recently been found in a siliceous shale in the Tindir Group in eastern Alaska. This tissue-grade metazoan fossil is of unusual interest because of the apparent late Precambrian age of the rock and because flatworms are thought to represent an important stage in the development of other metazoan groups. Morphologic features in Brabinthes suggest ancestry among the medusoid cnidarians.

INTRODUCTION

Attempts to document the early development of metazoan animals with fossil evidence are hampered by the poor chances for preservation of the soft-bodied organisms involved. The evolution from presumed colonial or multinucleate protistan precursors, to tissue-grade metazoans (without organ systems or a coelom), to organ-grade coelomate metazoans is generally accepted to have involved small forms without hard parts and to have taken place during late Precambrian time, between perhaps 750 to 680 m.y. ago. Various scenarios have been proposed for animal evolutionary pathways taken during this critical, heretofore undocumented, period in biologic history; these were conveniently summarized and referenced by Cloud (in Drake, 1968).

This report deals with a remarkably well-preserved microscopic fossil flatworm recently found in the Tindir Group, for which a Precambrian age is established in the type area. This acelomate, tissue-grade animal, less than 0.5 mm in length, has morphologic features of particular interest in terms of levels of metazoan organization considered important in the development of higher metazoans on the one hand and, according to Hadzi (1963) and others, of cnidarians (corals and jellyfish) on the other hand.

Implications of this and co-occurring fossils (C. W. Allison and others, in prep.) to late Precambrian biostratigraphy and evolutionary paleobiology are both significant and several. Although fossil evidence has not been previously found, it is almost certain that organisms of the nature represented by these Tindir fossils were developed by late Precambrian time.

OCCURRENCE AND PRESERVATION

Brabinthes churkinii (new genus, new species) occurs in the Nation area in black siliceous marine shale in the basalt and red beds, the middle of five units recognized in the Tindir Group by Brabb and Churkin (1969). According to these authors, the top of the basalt and red bed unit lies about 1,580 m stratigraphically below fossiliferous Lower Cambrian rocks in the Tindir type area to the southeast. The stratigraphic position of the flatworm-bearing volcanic sequence has been summarized by Earl E. Brabb and Michael Churkin, Jr. (written commun., 1975) as follows: “The [fossiliferous] volcanic sequence consists of mainly lithic tuff breccia with subordinate interbeds of shale, argillite, quartzite, chert, and limestone. The beds are extensively folded and, in places, highly sheared. Assignment of this volcanic sequence to our basalt and red bed unit of the Tindir Group is based on general lithologic similarity, structural considerations and the absence of obvious megafossils in an area where most Paleozoic rocks are easily distinguished by their fossil content.”

New evidence supporting a Tindir age assignment of the Nation area volcanic sequence has become available during the past year. First, presumed Tindir rocks in contact to the south are now known to include a dolomitic sequence clearly correlative with Brabb and Churkin’s (1969) Tindir dolomite and shale unit, which immediately underlies the basalt and red bed unit in the type area (Gary L. Kline, oral commun., 1975). Second, over 50 thin sections of organic fine-grained rocks, representing 36 different horizons spread through two outcrop belts of the Nation volcanic sequence, have now been examined by me. Fifteen of these horizons contain microscopic fossils of very primitive plants or animals. In view of the fact that a rich variety of plant and animal fossils occurs widely in the unusually complete Paleozoic record in the vicinity (including rocks similar to those of the volcanic sequence but lacking obvious fossils), it is reasonable to
suggest that absence of any trace of the rich local Paleozoic plant and animal biotas in a sequence that has preserved a variety of much more delicate forms is because these more highly evolved Paleozoic organisms had not developed by the time of deposition of these Tindir rocks.

The Tindir basalt and red bed unit has been correlated by several workers with the Rapitan Formation in northwestern Canada, for which a Precambrian age of <850 m.y. is proposed (Gabrielse, 1967; Stewart, 1972).

Brabinthis churkini is three-dimensionally preserved and is remarkably undistorted and complete. In preparation of the thin section, the upper and lower (dorsal and ventral) surfaces have been ground away such that mesenchyme is represented in most of the body both above and below the level of the gut, and structure of the head area above this level is observable. Body outline is clearly marked by a colorless outer tissue layer in which no evidence of nuclei or cell membranes has been seen. The mesenchyme layer is readily distinguishable by its brownish color and minutely dotted, homogeneous appearance. The specimen has been studied and photographed with light microscopy in ordinary transmitted light.

DESCRIPTION AND INTERPRETATION

Class Turbellaria
Order and family uncertain

Brabinthis new genus

Body elongate, with flattened anterior and paired anterior-lateral projections and round tail; mouth anterior, below center of head; gut straight, very narrow, extending into tail and toward anterior projections; single, simple (?) reproductive bursa located behind head; epidermal and mesenchyme tissues apparently syncytial; statocyst, brain, frontal gland complex, anus, gonads, gonopores, penis, excretory structures, nerve cords, cilia, rhabdites, and epidermal sensory structures not observed. Type species: Brabinthis churkini.

Brabinthis churkini new species

(Fig. 1; Table 1)

Body slightly widened behind head, narrowing into tail of essentially constant diameter; apparent reproductive bursa on right side close to head, open laterally above gut, open to intestine from above and possibly also posteriorly; gut slightly widened in main body and in canals directed toward lateral projections (auricles); epidermal layer about 2 μm thick; mesenchyme present everywhere in body below epidermis except in gut and other body cavities. Holotype: U.S. National Museum 220052. Occurrence: lat 65°13.5′N, long 142°17.5′W, basalt and red beds unit, Tindir Group, east-central Alaska. The genus and species are named for Earl E. Brabb and Michael Churkin, Jr., U.S. Geological Survey.

A number of morphologic features in Brabinthis churkini are of interest in terms of early turbellarian development, including especially the nature of body tissues and character, or absence, of various other structures. It is important in interpretation of these to emphasize that we are dealing with a fossil. Nerve cords, cell membranes in the tissues, cilia, and epidermal sensory structures, for example, may have been present but not preserved. Continuation of the gut beyond the point of flexure in the tail is not certain because the tip passes down into the rock slice and is thus not clearly seen. Basal and circumintestinal membranes may be postulated on the basis of the more or less well-defined margins between these layers, but margins of the presumed reproductive bursa and most other cavities are definitely less marked. This circumstance is associated with the fact that presence of the bursa and some head-area structures is marked in the fossil by absence of mesenchyme in the appropriate positions; not be observation of tissues clearly belonging to these structures. For this reason, an unequivocal statement of whether or not a brain, frontal gland complex, or statocyst in particular were present is not warranted on available evidence.

Distinctive margins of the mesenchyme at the bases of the anterior projections as seen in the photographs are notable; however, examination at high-power magnification reveals a thin layer of mesenchyme crossing from the head into the anterior and right-lateral projections. Extension of the enteric cavity above the mouth may include space for a statocyst, though no evidence of a membrane that might be expected here is observable. Lateral outpocketings of the gut from the center of the head are slightly wider and less regular than that passing anteriorly. Although not clear in detail, there is a short um in the median sagittal axis passing forward from the base of the anterior projection (Fig. 1b). This originates at the level of the gut as do the lateral outpocketings, which show at different focal depths because the specimen lies slightly oblique to the plane of the thin section with its right side lower than its left side. Paired canals apparently present along the median sagittal axis above the gut at the anterior end of the head (Fig. 1c) may have accommodated epidermal sensory or statocyst structures.

Interpretation of the sac-like cavity behind the head as a reproductive bursa is suggested because no other explanation seems likely in view of the otherwise very complete preservation of the specimen. As shown in Figure 1d (left), this bursa opens laterally above the level of the gut. At a lower level, a very thin layer of apparent mesenchyme separates it from the gut, but at this level the bursa appears to open posteriorly and centrally into the gut (Fig. 1d, right). The more or less oval, sac-like area behind the bursa suggested in Figure 1d (center) is not convincing as a distinct structure when viewing the specimen; presence of a clear mineral grain above indicates that it is an optical artifact.

An incomplete oval-shaped specimen 24 μm wide and 230 μm long, consisting only of mesenchyme rimmed with a clear layer 2 to 3 μm thick, found in another thin section of the same horizon as the type specimen of Brabinthis churkini, probably represents a slice from the ventral or dorsal surface of another individual of this species.

EVOLUTIONARY CONSIDERATIONS

Brabinthis churkini can be referred with reasonable certainty to the phylum Platyhelminthes and class Turbellaria. Many lower metazoon specialists consider the order Acoela (typically oval, very simple worms with syncytial tissues, no gut, and more or less centrally placed mouth) to represent the most ancient turbellarians (Karling in Riser and Morse, 1974; Hyman, 1951). Others maintain that the Acoela are secondarily simplified from progenitors with a gut and cellular body tissues (Ax in Dougherty, 1963). The body shape and the distinct gut present in Brabinthis clearly are not consistent with the original morphology of typical Acoela, but the

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<th>Table 1. Measurements of Holotype of Brabinthis Churkini</th>
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<td>Anterior tip to end of tail</td>
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<td>Center of head to tip of last article</td>
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<td>Center of head to tip of anterior projection</td>
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<td>Center of head to center of reproductive bursa</td>
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<td>Body width behind head</td>
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apparent noncellular tissues and the great simplicity, or absence, of other structures usually present or more complex in turbellarians do suggest a primitive level within the class.

There is agreement among many students of the lower metazoa that turbellarians are close to a stem position in the evolution of higher platyhelminths and thus to at least some organ grade and coelomate groups, the so-called higher metazoa. However, there is continuing disagreement as to the phylogenetic relationship of the Turbellaria and the Cnidaria (Hadzi, 1963; Steinböck in Dougherty, 1963). A persuasive array of evidence supports a hypothesis of development of the Turbellaria from a planuloid organism (Hand in Dougherty, 1963; Hyman, 1951). Other evidence, in part also persuasive, supports evolution of the Turbellaria directly from ciliated, multinucleate protostians (Hadzi, 1963). Several proponents of the latter hypothesis (Hadzi, 1963; Steinböck in Dougherty, 1963) further concluded that the Cnidaria evolved from an early turbellan stock. Inasmuch as Brabbinthes appears to be the oldest known, and a very early, turbellan, it is important to consider ways in which it may shed light on these questions.

The well-developed tail, ventral mouth, and flattened body and anterior projections in Brabbinthes indicate an active benthic existence. Presence of a very thin mesenchyme layer and absence of other structures in the auricles in particular suggest flap-like projections used primarily in swimming or gliding above the bottom. Although it may have functioned also in association with a swimming mode of life, need for such a long anterior projection, which is essentially identical to but somewhat longer and thicker than the auricles, is not so readily discernible in an animal otherwise well adapted for forward movement.

Auricles and some form of anterior projection, although not similar to those in Brabbinthes, are present in various modern turbellarians, including tentacles in the Temnocephala. These are generally not considered to reflect descent from ancestors with such structures. However, Hadzi (1963), although not proposing the Temnocephala as directly ancestral to the actinarians, which he considered the most ancient Cnidaria, did suggest that this group might exemplify a pattern followed in turbellarians to actinian evolution. An alternative evolutionary sequence is that from planuloid to Cnidaria and, separately, to acel turbellarians as supported by Hyman (1951), or planuloid to Turbellaria (not necessarily an acel) as supported by Hand (in Dougherty, 1963). This history requires that the oral-aboral axis of the planuloid, while retained in the adult Cnidaria, is not retained in the Turbellaria, because in the latter the original oral pole is shifted anteriorly in even the most primitive representatives herefore known or postulated.

Acceptance of a planuloid stock as ancestral to turbellarians, or both turbellarians and cnidarians, can accommodate the suggestion that a tendency to develop tentacle-like projections was present in the ancestral stock. The three anterior projections in Brabbinthes could then be readily explained as newly developed features adaptive to an active mode of life in a bilateral animal. Such a sequence does not absolutely rule out descent of Brab-

Figure 1. Brabbinthes churcini (new genus, new species), USMN 220052, holotype. Photomicrographs in ordinary transmitted light. (a) Composite of entire specimen at level of gut. Anterior and right lateral projections and end of tail dip into rock away from observer. (b) Anterior portion of head and base of anterior projection. (c) Head and base of left lateral projection shown, left to right, as increasing focal depth. (d) Right lateral area of head and reproductive bursa shown, left to right, as increasing focal depth. (e) Tail at level of gut; flexure in tail is in upper right corner of photograph. Bar scale for (a), 100 μm; for (b) through (e), 25 μm.
binthes from an acocel turbellarian, but whether or not it is derived directly from a planuloid or via the Acoela, this order of descent does not provide a convincing explanation for the distinctive nature and similarity of the three anterior projections in Brabinthes, and especially it does not provide a convincing explanation for the three intestinal extensions associated with them. It is also not consistent with the fact that, presuming this specimen of Brabinthes is not a larval form, its oral-aboral axis is not shifted from the planuloid condition. These features seem to suggest that a different interpretation of the ancestry of the critical turbellarian group, which is commonly postulated to represent the earliest truly bilateral animals, should perhaps be considered.

It is not particularly difficult to conceive of a small, simple medusa in which the mesenchyme, and to some degree also the enteron, extended into four rather firm tentacle-like projections and in which fertilization and, at least in part, embryologic development was internalized. This organism would, as an adult, have some morphologic resemblance to certain modern cnidian actinula larvae. If such an animal adopted a preferred direction of movement, followed by flattening and increased development in size and physiologic function in the trailing “tentacle,” with concomitant reduction and change in primary function in the leading and lateral “tentacles,” it would approach the morphology of Brabinthes. This order of descent would explain the similarity of the three anterior projections in Brabinthes and the enteric canals associated with them as reduced, originally equal structures. It would also indicate that the adult oral-aboral axis in early flatworms may have been that of the planuloid via an actinuloid intermediary.

This hypothesis would, in effect, shift ancestry of the Turbellaria from a pre-cnidarian to an early cnidarian stock, that is, from one unidentified adult precursor, the planuloid, to another, the actinuloid. A number of features consonant with this interpretation are found among the trachyline hydrozoan cnidarians, including tetramerous symmetry, polypod generation absent, an apical sensory structure, firm tentacles that may stand out from the upper surface and have a gastrodermal core, mouth opening directly into a “stomach” with four outpocketing radial canals, gonads along the radial canals, fertilization and embryologic development internalized and, in one case (Hyman, 1951), sexes not separate. Not all of these features are present in any single modern representative, but they have all been expressed within the trachyline stock.

Larval development in modern trachylines also provides some evidence of interest in this regard. In a common sequence from the Trachymedusa planuloid larva to medusa, the swimming planuloid develops a mouth and tentacles and becomes an actinula; medusoid development then follows by radial expansion, invagination between the mouth and tentacles to form the sub-umbrella and, finally, the bell and its marginal structures form (Hyman, 1941). The body of the trachyline Narcomedusa actinula larva also first represents only the aboral part of the future adult, with the oral portion and bell growing out later such that the first set of tentacles is left behind on the bell (Hyman, 1940). Free-swimming larvae are known among the Turbellaria in the polyclads, including types with four or eight ciliated lobes. This pattern is not characteristic of the few other turbellarians for which embryologic development is known; however, embryologic development in most other modern turbellarians is thought to be considerably modified from an original mode closer to that of the polyclads (Hyman, 1951).

In view of the known morphologic flexibility in cnidarians, it seems possible that an early representative of this group, with enteron extended into four radial tentacle-like projections, adopted a preferred direction of anterior movement, thereby suppressing development of a bell and initiating bilateral development that could follow the consequences suggested above. It is of interest to note that the trachylinids have been suggested as the most primitive living cnidarian stock (Hyman, 1940) and that fossils referred to this group appear early in the known record.

Regardless of which scenario one favors for the origin of the Turbellaria, there is little doubt that attainment of the level of development of this group was a major event in biologic history. Fossil evidence bearing on the timing of this key step includes the impressions of megascopic soft-bodied animals, including cnidarians and segmenteans, presumably coelomate organ grade organisms of annelid affinities, in the sub-Cambrian Ediacarian biota from Australia and elsewhere (Glassner and Wade, 1966; Glassner, 1971). These range in age from about 600 to 680 m.y. and are thus older than the highly varied shelly fossils widely present in Lower Cambrian rocks. Well-documented fossils of unequivocally earlier age are microscopic and of primarily, if not exclusively, algal, fungal, and bacterial affinities.

On the basis of available fossil evidence, then, differentiation of the early metazoa took place before attainment of the coelomate organ-grade level represented among Ediacarian fossils. Logic dictates that small, tissue-grade metazoans would have preceded these. “Animal” protists, which certainly can be expected to have appeared before the Ediacarian biotas, have not yet been reported from Precambrian rocks. However, a variety of microscopic fossils, generally ill-defined but simple and below tissue grade, that occur in the rock sequence yielding Brabinthes may well represent such organisms; these and other mostly incomplete tissue-grade metazoan fossils in Tindir samples are undergoing further study by me and by others.

REFERENCES CITED


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